FOOD HABITS AND DIETARY OVERLAP OF NONGAME INSECTIVOROUS FISHES IN FLINT CREEK, OKLAHOMA, A WESTERN OZARK FOOTHILLS STREAM[1]

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Abstract.—Insectivorous fishes were sampled from March, 1983 to February 1984, in Flint Creek, Delaware Co., Oklahoma. There was insignificant habitat segregation between *Etheostoma spectabile* and *E. punctulatum* and seasonal habitat partitioning between *Cottus carolinae* and both darters. Mature *E. spectabile* ate primarily chironomids and mayflies, whereas juveniles fed primarily on microcrustaceans. Mature *E. punctulatum* consumed fewer *Ephemerella* and *Leptophlebia* than *E. spectabile*, feeding on *Stenonema* and other crustaceans. Juvenile *E. punctulatum* fed mainly on amphipods and mayflies, and juvenile *E. spectabile* ate primarily microcrustaceans. *Cottus carolinae* elected primarily mayflies in spring-summer and chironomids in January-February. Coefficients of dietary overlap were highest between larger *E. spectabile* and juvenile *E. punctulatum* and lowest between immature *E. spectabile* and mature *E. punctulatum*. Overlap between the two darters was significantly correlated with differences in mean prey size ($p<0.0005$). Overlap between sizes of *E. spectabile* was also significantly correlated to differences in mean prey sizes. *Etheostoma spectabile* generally preferred smaller prey than *E. punctulatum*. All three species avoided *Stenelmis*. *Cottus carolinae* avoided microcrustaceans. The study showed that resource partitioning among these three insectivorous fishes is affected by complex interactions of habitat and prey electivity, and prey size selectivity.

Darters and other nongame insectivorous fishes, such as sculpins and madtoms, are often found coexisting in the same stream (Diaber 1956, Braasch and Smith 1967, Page and Smith 1970, 1971, Novak and Estes 1974, Page 1974, Flynn and Hoyt 1979, Matthews et al. 1982, Wynes and Wissing 1982). In such systems, resource partitioning by coexisting species is expected (Gause 1934, Zaret and Rand 1971). Smart and Gee (1979), Matthews et al. (1982) and Wynes and Wissing (1982) have shown varying degrees of segregation of food and habitat use in coexisting darter species. Northcote (1954) studied the ecology of two sculpin species, and Daiber (1956) compared the feeding habits of the mottled sculpin and the fantail darter. Ecological segregation has also been shown among several other groups of sympatric freshwater fishes (Zaret and Rand 1971, Moyle 1973, Mendelson 1975, Werner and Hall 1976, Surat et al. 1980, Baker and Ross 1981).

Several factors may influence competition for food between cohabiting fishes. These include primarily: (1) the utilization of different habitats, (2) prey size selectivity, and (3) the selection of specific prey species.

Spatial segregation by stream fishes is difficult to assess, and studies based on seine hauls may be deceptive, since the method of capture potentially disturbs them to the point where their distribution may no longer represent natural activities, or the sampling area is so large that important differences in microhabitat usage are obscured.

The food habits of some darters and sculpins change as they mature (Koster 1937, Bailey 1952, Daiber 1956, Braasch and Smith 1967, Page and Smith 1970, 1971, Scalet 1972, Page 1974, Flynn and Robert 1977, Schenec and Whiteside 1977, Layzer and Reed 1978). This suggests an age-related change in the strategies of food partitioning. Different size classes of a species are often found in different habitats. This potentially reduces both interspecific and intraspecific competition. The selection of different prey or different prey sizes may be influenced by many factors such as morphological, physiological, and behavioral characteristics of both the predator and prey.

Preliminary studies of darter food habits in Flint Creek, Oklahoma, suggested a difference in the magnitude of dietary overlap, depending on the size classes of fishes compared. Although Smart and Gee (1979) separated fish into age groups, most studies have reported indices of overlap without sub-

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dividing the population into size classes, pos- sibly overlooking some very important as- pects of darter ecology.

At times during the life histories of game fishes there may be competition with noneco- nomic fishes for the available food resources. To better comprehend these relationships, it is necessary to understand the resource re- quirements of the noneconomic species. In Flint Creek, Delaware County, Oklahoma, insectivorous fishes that are in potential com- petition with the primary game fish, the smallmouth bass (*Micropterus dolomieui* La- cepede), are the orangethroat darter (*Etheo- stoma spectabile* Agassiz), the stippled darter (*Etheostoma punctulatum* Agassiz), the banded darter (*Etheostoma zonale* Cope), the fantail darter (*Etheostoma flabellare* Rafi- nesque), the greensided darter (*Etheostoma blennioides* Rafinesque), and the banded sculpin (*Cottus carolinae* Gill).

The food habits and life histories of many darters and sculpins have been studied (Koster 1937, Dineen 1951, Bailey 1952, Braasch and Smith 1967, Page and Smith 1970, 1971, Scalet 1972, Novak and Estes 1974, Page 1974, Flynn and Hoyt 1979, Cordes and Page 1980). Neither the food habits of the orangethroat darter, the stippled darter, or the banded sculpin nor the relation- ships between these species have been re- ported. Therefore, the objectives of this study were: (1) to describe the food habits of the three most abundant insectivorous fishes in Flint Creek, Oklahoma, *E. spectabile*, *E. punctulatum*, and *C. carolinae*; (2) to deter- mine the magnitude of dietary overlap be- tween various sizes of the two darter species and the banded sculpin; (3) to conduct field and laboratory studies to determine if the darters and sculpins of each size class are se- lecting prey items.

Materials and Methods

Study area. — Flint Creek is a third order stream running southeasterly through Dela- ware County, Oklahoma, to its confluence with the Illinois River. The study area was a 1-km section approximately 4-km upstream from Oklahoma Highway 33. At this point the stream passes through an open valley with occasional riparian trees. The stream consists of many pools separated by as many riffles. The substrate ranges from detritus and silt to gravel and rubble, with gravel being most common. During summer months, a large portion of the stream becomes covered with water willow (*Justicia americana*) and water primrose (*Ludwigia* spp.).

Habitat usage. — Fishes were captured monthly from March 1983 to February 1984 using a kick-net placed downstream of habi- tats to be sampled, with the substrate dis- turbed to dislodge fish. A total of 50 kick-sets were made monthly in each of four general habitats: (1) open pools, (2) open riffles, (3) pools with submerged and/or emergent cover, and (4) riffles with submerged and/or emergent cover. The standard length in mm was measured for each fish. An analysis of co-dispersion was made incorporating a log- likelihood ratio test. Although sampling effi- ciencies may have differed in each habitat, an ANOVA was run to test for differences in the average length of each species between the four habitats followed by a Student-Newman- Keuls multiple comparison.

Stomach analysis. — In habitats where two or more species were captured, five fish in as many 10-mm size classes as possible were pre- served in 10% formalin for stomach analysis. Roberts and Winn (1962) and Daughtery et al. (1976) found that visual stimuli were neces- sary for normal feeding responses of darters. Several researchers have found darters to ex- hibit diurnal feeding patterns, with peak feed- ing occurring in midday or afternoon, with maximum gut content later in the day (Mathur 1973, Schenec and Whiteside 1977, Layzer and Reed 1978, Cordes and Page 1980, Matthews et al. 1982). Preliminary studies indicated the two darter species under study both fit this pattern; therefore, all fish were captured between 12:00 noon and 5:00 p.m.

Stomach contents of the preserved darters were identified to the lowest possible taxon (genera for most insects). The head capsule width (HCW) of insects or the maximum di- ameter of other taxa was measured with an ocular micrometer.

Food availability. — Within the same habitats where darters were collected for stomach analyses, three 0.05 m^2 Hess samples were taken at the same monthly sampling times and preserved in 70% isopropanol for

determination of prey availability. Additional benthic organisms were collected, and their HCW or maximum diameter measured. These organisms were then killed in 4% for- malin, immediately dried for 24 hours at 105 C, and their dry weight was measured to the nearest 0.1 mg. Regression lines were devel- oped from these data and were used to esti- mate the live dry weight of the prey con- sumed.

DIETARY OVERLAP. — Dietary overlap was determined with an index of association $C\lambda$ (Horn 1966) which is calculated:

$$C\lambda = \frac{2\sum_{i=1}^{s} x_i y_i}{\sum_{i=1}^{s} x_i + \sum_{i=1}^{s} y_i}$$

where:

s = total number of food taxa

x_i = proportion of the total diet of species x taken from taxa i

y_i = proportion of the total diet of species y taken from taxa i

This index ranges from 0.0 to 1.0, with a value of 0.0 indicating no overlap, and 1.0 indicating complete overlap. An index of overlap was calculated for both numbers and biomass of each prey taxa.

PREY SELECTION. — A linear index of food selection L (Strauss 1979) was used. It is calcu- lated:

$$L_i = r_i - p_i$$

where:

r_i = the relative abundance of item i in the gut

p_i = the relative abundance of item i in the environment

This index ranges from -1.0 to 1.0, with posi- tive values indicating preference and negative values indicating avoidance and/or inaccessi- bility. A Students t-test was used to test the null hypothesis of no difference in L from zero.

An index of selectivity assesses differences in the proportions of a specific prey item in the diet relative to proportions available in the environment. These indices may or may not express actual election or avoidance of a prey item. The real availability of prey items is usually not known; therefore, unavailability may be mistaken as avoidance.

The following experiment was conducted in June 1984 to gain some further insight into selectivity by darters in a situation where no prey had protective cover. Five 18.9-1 aquaria were placed in the stream to minimize stress on the darters during the experiment. A selected group of prey, representative of the stream population and in sufficient numbers ($n=70$) to allow feeding without greatly affect- ing the proportions of the prey, were counted into the aquaria. Fish were placed in the aquaria after dark as follows: (1) two mature E. spectabile in each of three aquaria and (2) two mature E. punctulatum in each of two aquaria. This allowed adjustment to confine- ment prior to dawn, when normal feeding should begin. The darters were allowed to feed until noon, when they were preserved for stomach analysis.

SIZE SELECTIVITY. — Size selectivity was as- sessed by comparing mean widths of prey consumed by each species in each size class. A one-way ANOVA followed by a Student-New- man-Keuls multiple range test was used to test for differences in mean widths of prey consumed between different size classes of fishes.

RESULTS AND DISCUSSION

SEASONAL ABUNDANCE. — A total of 992 darters and sculpins were captured over the 12-month study period. *Etheostoma spectabile* was most abundant ($n=543$), fol- lowed by *Cottus carolinae* ($n=275$), *E. punc- tulatum* ($n=157$), and *E. zonale* ($n=17$). Their seasonal abundance from March 1983 to February 1984 is illustrated in Figure 1, and numbers of *E. spectabile* and *C. carolinae* generally followed expected survivorship, ex- cept in August when dense macrophytic vege- tation may have impaired sampling efficiency. These two species are spring and summer spawners, and their numbers were greatest, as expected, during these periods of recruit- ment. *Etheostoma zonale* was low in abun- dance over the entire year, with the greatest number captured ($n=6$) occurring in August. The efficiency of seining as a method of sam-
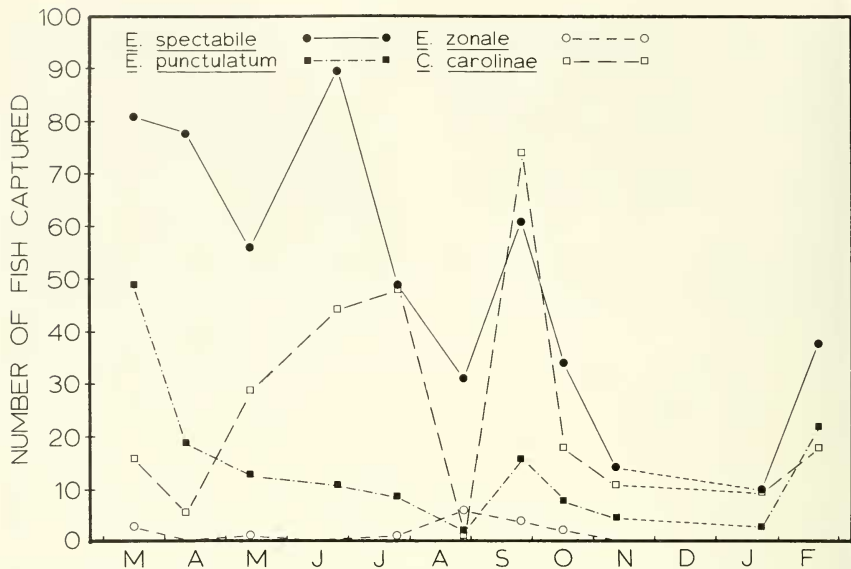
Fig. 1. Seasonal abundance of the four most abundant noneconomic insectivorous fishes in Flint Creek, Oklahoma, March 1983 to February 1984.

pling darters and sculpins is questionable, be- cause of their ability to avoid capture by hid- ing under rocks and in crevices. The use of kicknets in this study probably gave a more discrete sample.

HABITAT USAGE. —An analysis of co-disper- sion for *E. spectabile* and *E. punctulatum* re- vealed no significant habitat segregation. Sig- nificant ($p<0.05$) positive co-dispersion (overlap) was observed in June and Septem- ber 1983. All values for co-dispersion were positive except in November 1983 and Janu- ary 1984, when numbers collected were low (19 and 13, respectively).

Areas sampled can greatly affect the results of an analysis of co-dispersion. Small sampling areas tend to give negative values, whereas large sampling areas tend to result in positive values. Kick-netting resulted in a large per- centage of kick-sets capturing no fish. The positive values for co-dispersion and a low capture rate suggests that the two darters did not separate themselves on the basis of habitat selection alone.

Similar analyses with *C. carolinae* and both darters showed relatively more habitat segre-

gation between mature banded sculpins and both darters during spring (March, April), with significant negative co-dispersion be- tween *C. carolinae* and *E. punctulatum* in April. Significant ($p<0.05$) overlap was shown between *C. carolinae* and *E. spectabile* in May, coinciding with the hatching and re- cruitment of both species. Mature *C. caroli- nae* were absent from the four habitats sam- pled from May to September, when juvenile fish were abundant, probably reducing in- traspecific and interspecific competition.

On a yearly basis, an ANOVA revealed a significant difference in the average body lengths of both *E. spectabile* and *E. punctula- tum* between habitats ($p<0.0001$), whereas no significant difference in the mean lengths of *C. carolinae* were found. A Student-New- man-Keuls multiple comparison showed *E. punctulatum* with a significantly larger mean length in riffles with submerged and/or emer- gent cover than in open pools, 62.3 and 43.5 mm, respectively ($p<0.05$). *Etheostoma spectabile* had a significantly higher mean length in riffles with and without submerged and/or emergent cover (51.6 and 50.3 mm,
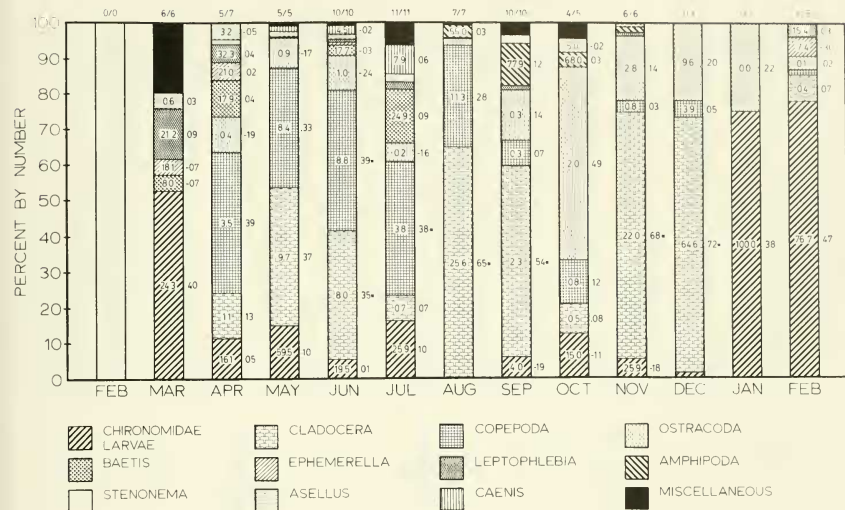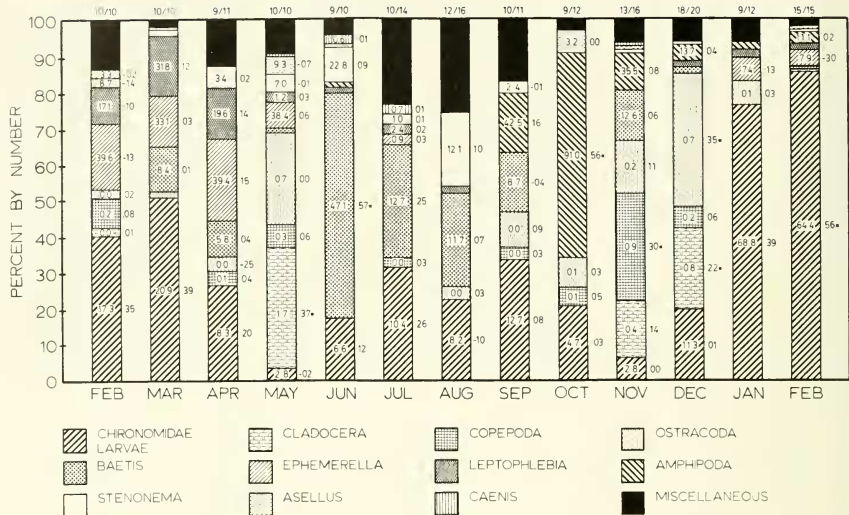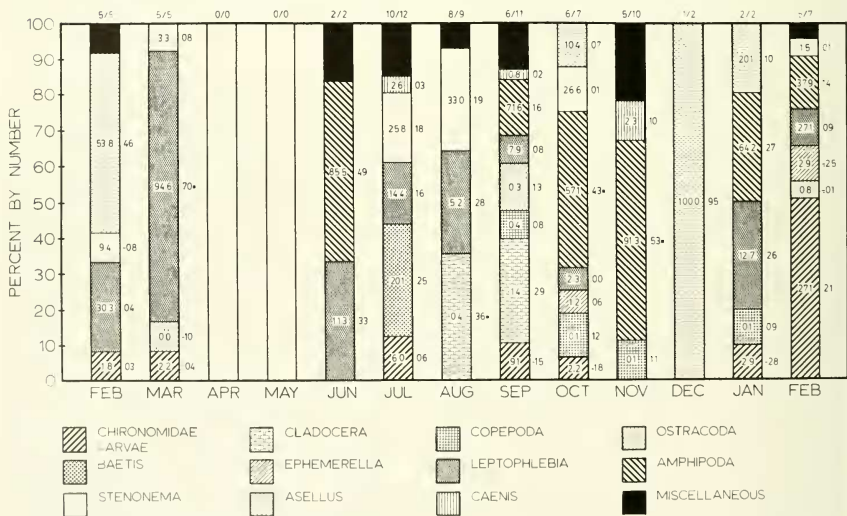
Etheostoma spectabile (<41mm)

Fig. 2. Food habits of *Etheostoma spectabile* <41 mm February 1983 to February 1984. In this figure and Figures 3–6, each bar equals the percent by number of each selected prey item, numbers above bars are equal to the ratio of fed to total guts examined, numbers within bars are equal to the percent by dry weight of food items, and numbers right of major food categories are equal to the Strauss Selectivity Index. Asterisks with Strauss Index are equal to significance ($p<0.05$).

respectively) than in pools with and without submerged and/or emergent cover (42.3 and 40.8 mm, respectively) ($p<0.05$). Although not significant, both species were larger in riffles with submerged and/or emergent cover and pools with submerged and/or emergent cover than in open riffles and open pools, respectively. The presence of different sizes of fishes in different habitats may be important in the reduction of intraspecific competition. Since roughly similar size classes of the two darters were found in similar habitats, the segregation of habitat alone by different size classes probably had little effect on interspecific competition; however, the combination of habitat selection, temporal segregation of spawning times, prey selection, and differences in prey size probably resulted in lowered competition between *E. spectabile* and *E. punctulatum*.

FOOD HABITS. —In both darters a major dietary shift could be related to maturation, and therefore separation of fish sizes for discussion of food habits was made on this basis.

Etheostoma spectabile and *E. punctulatum* were therefore respectively separated into <41 and >40, and <51 and >50 mm sizes (Figs. 2–5).

The stomachs of 244 *E. spectabile* contained 35 different prey taxa. Both juveniles and adults fed heavily on chironomids during winter and early spring (January–March, Figs. 2,3). Chironomids continued to constitute 16.1%–59.5%, by dry weight, of juvenile fish diets in April to July, as they increased feeding on microcrustaceans and small mayflies (Fig. 2). This shift to planktonic prey items coincided with recruitment of darter fry. In August, diets of these smaller fish were exclusively composed of microcrustaceans, particularly Cladocera and Copepoda, and for the rest of the year microcrustaceans and amphipods continued to make up the major percentages by number and dry weight, into December (Fig. 2). Mayfly nymphs (*Baetis, Stenonema, Ephemerella, Leptophlebia*, and *Caenis*) made up 49.1%–77.3%, by dry weight, of mature *E. spectabile* diets in spring

Fig. 3. Food habits of *Etheostoma spectabile* >40 mm February 1983 to February 1984.

Fig. 4. Food habits of *Etheostoma punctulatum* <51 mm February 1983 to February 1984.

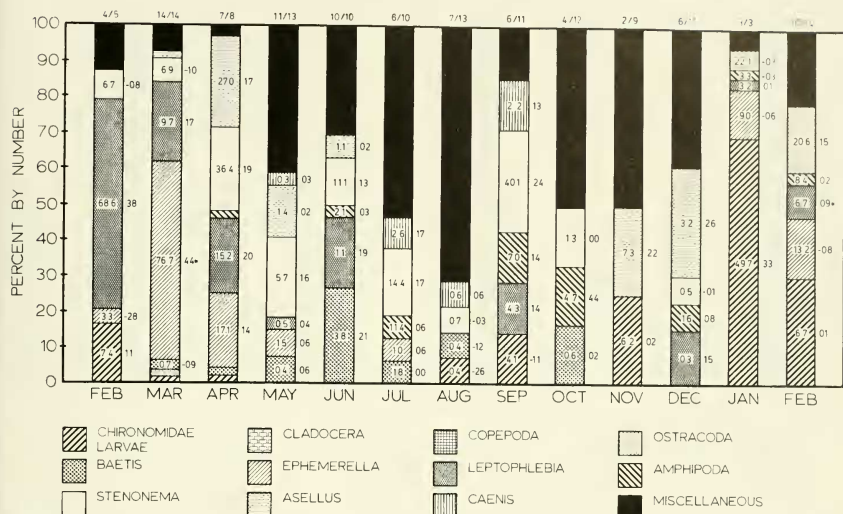## Etheostoma punctulatum (>50mm)

Fig. 5. Food habits of *Etheostoma punctulatum* >50 mm February 1983 to February 1984.

and early summer until June (Fig. 3), corre- sponding with the emergence and recruit- ment of these insects. They were ingested at lower levels for the rest of the summer, and none were eaten by 12 fish in October (Fig. 3). Unlike juveniles, mature fish fed on chirono- mids at levels less than 11% by dry weight from April to July, and microcrustacea were not present in mature fish guts in late spring and summer in amounts above 3.1% by dry weight (June, August). Amphipods appeared in diets of mature orangethroat darters at lev- els of 42.5% and 91.0% (dry weight), respec- tively, in September and October, when in- gestion of amphipods generally decreased and chironomid feeding increased in November and December until winter, when chirono- mids again predominated in guts. Mature fish relied more heavily on larger items such as *Baetis*, *Ephemerella*, *Leptophelebia*, *Ste- nonema*, and amphipods as these items were available.

Stomachs of 205 *E. punctulatum* contained 30 different prey taxa. Both classes of *E. punc- tulatum* utilized chironomids in the coldest months, January and February (Figs. 4, 5), but relied much less on them in those months,

and generally throughout the year, than did *E. spectabile* (Figs. 2, 3). Feeding by *E. punc- tulatum* during these months was less concen- trated on chironomids than in *E. spectabile*, in favor of diverse feeding on mayflies, *Asel- lus*, and amphipods (Figs. 4, 5).

Few juvenile *E. punctulatum* were cap- tured in spring (March–May). The five fed fish taken in March fed almost exclusively on the mayfly *Leptophlebia* (94.6% by dry wt.), apparently segregating themselves from small *E. spectabile* that spread their feeding pre- dominately over chironomids (24.3% by dry wt.), *Ephemerella* (18.1%), and *Lep- tophlebia* (21.2%). During summer months (June–September) and into November, juve- nile stippled darters fed mainly on amphipods and the mayflies *Stenonema*, *Baetis*, and *Lep- tophlebia*, further suggesting segregation of themselves from smaller *E. spectabile* that were feeding more on microcrustaceans dur- ing that time. The single fed immature fish captured in December had only *Asellus* in the gut (Fig. 4). Mature *E. punctulatum* showed little pattern in feeding, except in January to March, when chironomids, *Leptophlebia*, and *Ephemerella* were ingested in high vol-
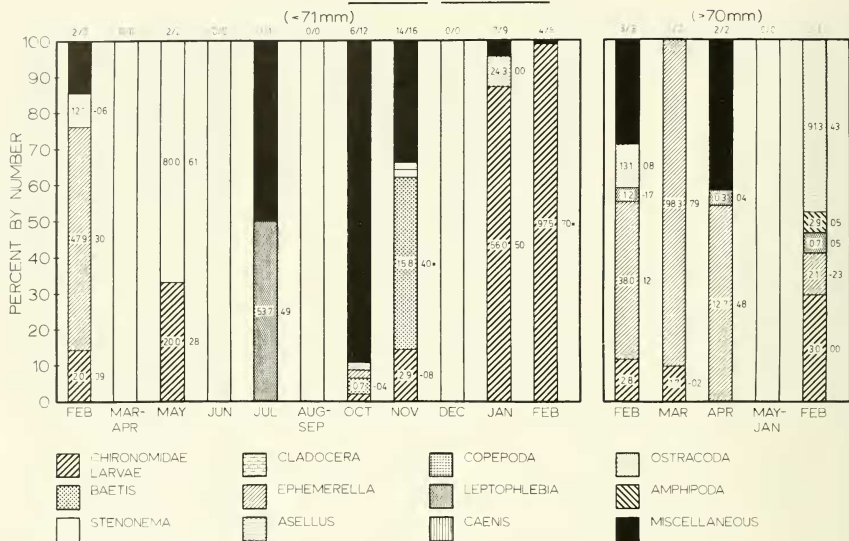
Cottus carolinae

Fig. 6. Food habits of *Cottus carolinae* February 1983 to February 1984.

umes (Fig. 5). During these months larger *E. spectabile* were feeding predominately on chironomids and the mayflies *Ephemerella* and *Leptophlebia*. Ingestion of *Stenonema* and miscellaneous organisms was greater and more seasonally distributed (Fig. 5) than in larger *E. spectabile* (Fig. 3), indicating partitioning of available food resources by the mature fish of both species. The seemingly erratic pattern of prey ingestion (Figs. 4, 5) was generally closely related to the relative abundance of the various prey in the environment.

A few taxa which were not consumed in sufficient numbers to be important items in the annual diet of both darter species composed a large percentage of the diet in months when these items were available. In March 1983 fish eggs made up 25.6%, by dry weight, of the diet of juvenile *E. spectabile*. In mature fish the following prey made up an important part of the diet: February 1983, *Prostoia* (12.8%); April 1983, fish eggs (18.3%), *Isoperla* (5.1%); August 1983, *Isonychia* (35.4%). The diet of smaller *E. punctulatum* contained such important prey as: July 1983, *Neoperla* (16.2%), *Stenacron* (9.8%); August 1983,

Corydalus (61.4%); September 1983, *Leptohyphes* (5.2%). The following items were important at times in the diet of mature *E. punctulatum*: May 1983, *Isonychia* (39.1%), oligochaeta (27.3%), *Psephenus* (8.2%), *Acroneuria* (15.2%); June 1983, decapoda (20.8%), *Acroneuria* (38.6%), *Corydalus* (16.4%); July 1983, *Neoperla* (17.9%), *Psephenus* (27.9%), decapoda (18.8%); August 1983, *Corydalus* (47.9%), decapoda (34.2%), *Psephenus* (13.7%); September 1983, *Psephenus* (42.4%); October 1983, *Argia* (15.2%), *Corydalus* (78.2%); November 1983, *Psephenus* (86.5%); December 1983, oligochaeta (94.3%).

Two size classes of sculpins were selected with similar reasoning as with the two darter species. These size classes were <71 and >70 mm (Fig. 6).

During the initial months of the study (February–April), it was not known whether sufficient sculpins could be sampled for food habits analysis; therefore, young sculpins were returned to the stream. In the fall, fish were collected for stomach analysis, and 42 specimens were taken during the period Oc-

tober–February (Fig. 6). Mature fish were not collected in the study area of the stream during May–September, and very few were captured until February, possibly because of migration into unsampled habitats such as deep pools. Therefore, food habits were determined from a relatively small sample of nine fish during February–April 1983 and February 1984 (Fig. 6). While studying the movements of sculpins, Bailey (1952) found that, although they usually remained within a radius of 46 m, some moved up to 144 m from the point of initial capture. Deep pools were always within this range in the study area.

Stomachs of 53 *C. carolinae* contained 18 prey taxa. Cladocerans, copepods, and ostracods were absent in the diets of both size classes of *C. carolinae*, suggesting segregation of this species from juvenile *E. spectabile* during August–December, when the latter fed heavily on these items. Both size classes of *C. carolinae* fed on *Ephemerella* (47.9% and 38.0%, by dry weight) during February 1983, as did mature *E. spectabile* (Figs. 3, 6). Mature *C. carolinae* continued to feed on *Ephemerella* through April, when no juveniles were collected. At this time, mature *E. spectabile* and *E. punctulatum* were observed feeding on the mayfly *Ephemerella* (Figs. 3, 5).

In May and July the three small fish collected fed on chironomids (May, 20.0% by dry weight) and small mayflies, *Stenonema* (May, 80.0%), and *Leptophlebia* (July, 53.7%) (Fig. 6); in July *Hydroptila* was also taken (46.3%). During October and November small mayflies such as *Baetis* (0.7% and 15.8%, respectively, by dry weight) were taken, with large numbers of *Psephenus* (2.5%), decapods (63.2%), and *Corydalus* (29.8%) in October. In November *Corydalus* (59.0%) and *Psephenus* (16.6%) made up a large percentage of the diet. Heavy feeding by small *C. carolinae* on chironomids was observed in January (56.0%), increasing to 97.5%, by dry weight, in February (Fig. 6). Although the larger size class consumed some chironomids in this month, *Asellus* made up 91.3% of the diet of the mature fish (Fig. 6). Only mature *E. punctulatum* also fed on *Asellus* at this time in amounts higher than 2 percent (Fig. 5).

DIETARY OVERLAP. —Monthly values for dietary overlap between different size classes of

darters and sculpins were highly variable, ranging from 0.00 to 0.99 for numeric data and 0.00 to 0.97 for dry weight data (Table 1). Based on numeric data, the lowest average monthly overlap value was between immature *E. spectabile* and mature *E. punctulatum* (0.22), whereas the highest average monthly overlap value was between larger *E. spectabile* and juvenile *E. punctulatum* (0.45). Variations in monthly overlap values may be attributed to differences in prey availability, gape size differences, or differences in prey size. No significant correlation between overlap values and prey availability, or differences in gape were shown; however, a significant (p<0.0005) correlation between the difference in mean prey sizes of the groups being compared and overlap values was found. This indicates that prey size selection is important in regulating possible competition for food between these insectivorous fishes in Flint Creek.

Indices of dietary overlap between the two size classes of *E. spectabile* were significantly correlated (p<0.05) to the difference in the mean size of prey selected by the two groups. Although mean prey size selection may be important in reducing intraspecific competition for *E. spectabile*, the indices of dietary overlap between the two size classes of *E. punctulatum* were not correlated with the differences in the mean prey size selected by the two size classes. This suggests that the regulation of dietary overlap between the two size classes of *E. punctulatum* is dependent on some factor besides prey size, such as actual election of specific prey items.

Dietary overlap was generally high (.81–.99) only between small banded sculpins and both classes of the orangethroat darters in January–February 1984, since both species fed heavily on chironomids (Table 1). Overlap values between the banded sculpin and *E. punctulatum* were generally low. A value of .96 by number, .93 by dry weight (Table 1), however, was found in January between juvenile *C. carolinae* and mature *E. punctulatum*, when both species were feeding on chironomids.

SIZE SELECTIVITY. —The selection of prey on the basis of size is important in the partitioning of Flint Creek food resources by orangethroat and stippled darters. During most

TABLE 1. Coefficients of dietary overlap of different size classes of *Etheostoma spectabile*, *E. punctulatum*, and *Cottus carolinae* from February 1983 to February 1984. Upper values are based on numeric data. Lower values are based on dry weights data.

Comparison		Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb
E. spectabile	<41 mm	—	.33	—	—	.01	.40	.58	.84	.16	.03	.00	.17	.87
E. punctulatum	<51 mm	—	.37	—	—	.00	.49	.02	.97	.88	.63	.00	.04	.55
E. spectabile	<41 mm	—	.20	.19	.01	.05	.16	.00	.13	.07	.04	.00	.92	.61
E. punctulatum	>50 mm	—	.40	.48	.00	.09	.06	.00	.20	.08	.04	.00	.76	.17
E. spectabile	>40 mm	.29	.38	—	—	.03	.75	.27	.46	.88	.35	.00	.21	.85
E. punctulatum	<51 mm	.28	.53	—	—	.05	.25	.12	.80	.84	.55	.00	.13	.63
E. spectabile	>40 mm	.47	.38	.53	.18	.63	.22	.25	.44	.34	.06	.04	.98	.58
E. punctulatum	>50 mm	.43	.67	.44	.12	.25	.20	.01	.15	.06	.00	.85	.87	.21
E. spectabile	<41 mm	—	.94	.42	.73	.08	.55	.01	.22	.29	.44	.62	.97	.99
E. spectabile	>40 mm	—	.78	.76	.18	.51	.60	.03	.77	.94	.47	.07	.92	.96
E. punctulatum	<51 mm	.48	.37	—	—	.31	.46	.10	.33	.40	.15	.48	.25	.75
E. punctulatum	>50 mm	.49	.13	—	—	.04	.41	.69	.15	.06	.05	.03	.33	.27
C. carolinae	<71 mm	—	—	—	.12	—	.03	—	—	.01	.02	—	.94	.96
E. spectabile	<41 mm	—	—	—	.23	—	.04	—	—	.00	.02	—	.81	.95
C. carolinae	<71 mm	.55	—	—	.12	—	.04	—	—	.01	.33	—	.98	.99
E. spectabile	>40 mm	.67	—	—	.14	—	.04	—	—	.00	.06	—	.87	.90
C. carolinae	>70 mm	—	.17	.09	—	—	—	—	—	—	—	—	—	.50
E. spectabile	<41 mm	—	.31	.07	—	—	—	—	—	—	—	—	—	.04
C. carolinae	>70 mm	.64	.32	.43	—	—	—	—	—	—	—	—	—	.50
E. spectabile	>40 mm	.74	.54	.12	—	—	—	—	—	—	—	—	—	.06
C. carolinae	<71 mm	.89	—	—	—	—	—	—	—	—	—	—	—	.44
C. carolinae	>70 mm	.87	—	—	—	—	—	—	—	—	—	—	—	.03
C. carolinae	<71 mm	.06	—	—	—	—	.25	—	—	.01	.04	—	.21	.77
E. punctulatum	<51 mm	.03	—	—	—	—	.23	—	—	.00	.01	—	.15	.42
C. carolinae	<71 mm	.15	—	—	.43	—	.00	—	—	.05	.32	—	.96	.50
E. punctulatum	>50 mm	.06	—	—	.10	—	.00	—	—	.42	.25	—	.93	.11
C. carolinae	>70 mm	.32	.01	—	—	—	—	—	—	—	—	—	—	.55
E. punctulatum	<51 mm	.25	.00	—	—	—	—	—	—	—	—	—	—	.04
C. carolinae	>70 mm	.22	.85	.38	—	—	—	—	—	—	—	—	—	.80
E. punctulatum	>50 mm	.08	.96	.05	—	—	—	—	—	—	—	—	—	.36

months there were significant differences (p<0.05) in the mean prey widths selected by *E. spectabile* and *E. punctulatum* (Table 2). Also, during many months there were significant differences in prey widths selected by the different size classes of each darter species (Table 2.). Differences in morphology may be partially responsible for these differences. *Etheostoma punctulatum* has the larger gape of the two species. However, in both species the mean prey size selected was not significantly correlated with gape size (p>0.05). In months when *C. carolinae* were sampled for stomach analysis, the size of prey selected by this species was generally similar to that consumed by immature *E. punctulatum*. During January and February 1984, when both *C.*

carolinae and *E. spectabile* were electing chironomids, prey size for these two groups were similar, possibly indicating a period of higher competition.

SELECTIVITY.—For each class of fishes, monthly electivity for particular prey items were variable; however, some trends are evident (Figs. 2–6). All classes of fishes avoided *Stenelmis*. A preference for specific prey items coincided with months when those prey items were abundant. *Etheostoma spectabile* generally preferred smaller items such as cladocerans and chironomids, whereas *E. punctulatum* generally preferred larger items such as mayflies, *Corydalus*, decapods, and oligochaetes. *Cottus carolinae* showed negative selection for microcrustaceans such as os-

TABLE 2. Mean prey size (mm) of different size classes of *Etheostoma spectabile*, *E. punctulatum*, and *Cottus carolinae* from February 1983 to February 1984.

Month	E. spectabile immature	E. spectabile mature	C. carolinae immature	C. carolinae mature	E. punctulatum immature	E. punctulatum mature
Feb	—	0.74	1.40	1.14	1.45	1.09
Mar	0.54	0.67	—	1.29	1.31	1.35
Apr	0.28	0.92	—	1.47	—	1.38
May	0.11	0.36	0.98	—	—	2.30
Jun	0.13	0.68	—	—	0.84	1.49
Jul	0.23	0.55	0.55	—	0.93	2.14
Aug	0.07	0.65	—	—	0.83	2.73
Sep	0.21	0.35	—	—	0.36	1.66
Oct.	0.19	0.58	1.33	—	0.80	1.37
Nov	0.08	0.25	1.41	—	0.82	2.63
Dec	0.05	0.19	—	—	1.15	1.47
Jan	0.24	0.39	0.36	—	0.81	0.52
Feb	0.32	0.38	0.30	1.21	0.54	0.89

tracods and cladocerans, preferring mayflies, oligochaetes, and decapods.

Several researchers have suggested that changes in the diets of darters occur in re- sponse to changing prey densities (Braasch and Smith 1967, Page and Smith 1971, Page and Burr 1976, Schenck and Whiteside 1977). The results of this study support this conclu- sion. However, changes in either morphology or behavior, or both, as darters mature may also contribute to shifts in the diet. For exam- ple, the greater and more seasonally dis- tributed ingestion of *Stenonema* and other miscellaneous organisms by mature *E. punc- tulatum* (Fig. 5) than by mature *E. spectabile* (Fig. 3), and other instances of positive elec- tivity (Figs. 2–5), cannot be totally rational- ized on the basis of those food items becoming more available at certain times.

IN-STREAM AQUARIA EXPERIMENTS.—A group of natural prey, totaling 70 individuals in each aquarium, was used for assessing darter selectivity under the condition of no protective cover. Specific potential prey and their predetermined compositions (by num- ber) were *Cheumatopsyche* (14.3%), *Atherix* (28.6%), *Neoperla* (28.6%), *Stenelmis* larvae (7.1%), *Psephenus* (7.1%), *Isonychia* (7.1%), and *Stenonema* (7.1%). Under these condi- tions in June 1984, prey selection by the ma- ture fish of each species generally corrobo- rated selectivity indices calculated from field studies in June 1983. Positive election for mayflies and negative selection for *Psephenus* continued. Both species continued to avoid *Stenelmis*, and none were consumed. *Atherix*, which was not abundant in the

stream in June 1983, was also completely avoided. *Etheostoma spectabile* had a higher selectivity index for *Cheumatopsyche* (.11) and *Neoperla* (.13) than in the field studies (.01 and −.00, respectively). *Etheostoma punctulatum* also showed a higher index for *Neoperla* (.21) than in the field (−.00). The inaccessibility of *Cheumatopsyche* and *Neop- erla*, because of their cryptic nature and the fact that the experimental array of prey was not exactly the same as in the field, may have resulted in altered electivities.

CONCLUSIONS

Several factors influence the degree of over- lap in the diet of cohabiting fishes. Differ- ences in the diets of *E. spectabile*, *E. punctu- latum*, and *C. carolinae* in Flint Creek, Oklahoma, are related to a complex of factors, including the utilization of different habitats, prey size selection, and the selection of specific prey items.

The absence of mature *C. carolinae* during the summer and fall suggests their movement into unsampled areas, thereby exhibiting habitat partitioning. Analyses of co-dispersion further revealed partitioning of habitat be- tween the banded sculpin and both darters during months when mature sculpins were captured in the study area. Habitat partition- ing probably reduces both intraspecific and interspecific competition.

An analysis of co-dispersion between the two darters showed no habitat segregation; however, different lengths of both darter spe- cies were found in different habitats. This not

only may reduce intraspecific competition, but, together with temporal segregation of spawning times, may reduce interspecific competition.

The selection of prey on the basis of size was found to be an important factor in explaining overlap in the diets of insectivorous fishes. Other researchers have shown prey size to be consistent with gape (Northcote 1954, Daiber 1965, Matthews et al. 1982), and the results of this study support this. However, no correlations between mean prey size and gape were found. No significant ($p<0.05$) correlation was found between differences in gape and dietary overlap between corresponding fish groups. This suggests that gape may be important in prey size range, but other ethological or morphological factors are involved in the determination of the degree of dietary overlap between species. The selection of prey on the basis of size may reduce both intraspecific and interspecific competition. Although difference in dietary overlap between age groups of *E. spectabile* are correlated with differences in mean prey size, differences in dietary overlap between age groups of *E. punctulatum* and mean prey size are not.

Etheostoma spectabile generally fed upon smaller prey than *E. punctulatum*. Although the selection of prey items may be due to the election of a specific prey size, some selection of specific prey items regardless of size was noted. Both species selected prey at times when the particular item was abundant.

The management of stream game fishes is dependent on a knowledge of the species to be managed and their potential competitors. The resources available for management are dependent on the entire food web in the stream, and the resource requirements of noneconomic fishes are often overlooked, obscuring an important factor in total stream management. This study reveals food and potential habitat resource use by, and interactions between, nongame fishes in an Ozark stream. These findings not only provide new basic knowledge for these fishes, but they should be helpful reference data for future assessments of resource use, partitioning, and consequent development of management strategies for stream fishes.

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